Cost-effectiveness of Philippine butterfly species used in live exhibits: an assessment of longevity, encounter rate and behaviour.

Laura J. Robson
Dept. of Environmental Biology, University of Guelph, Guelph, ON N1G 2W1, Canada[1]
laurarobs@gmail.com

Adrienne Brewster
Wings of Paradise Butterfly Conservatory, 2500 Kossuth Rd, Cambridge, ON N3H 4R7, Canada
adriennebrewster@gmail.com

Gard Otis
Dept. of Environmental Biology, University of Guelph, Guelph, ON N1G 2W1, Canada
gotis@uoguelph.ca

Abstract. The importation of pupae represents a major cost for live butterfly exhibitors. Because captive butterfly species differ in life history characteristics, they should also differ in their value to exhibitors. Ten species of Philippine butterflies were imported to Wings of Paradise® Butterfly Conservatory. Butterflies were marked upon emergence as adults and were then released into the conservatory. Recaptures occurred three times daily, two to five times per week, from mid July to September, 2006. Using maximum likelihood estimation, we determined mean species longevity, encounter rate and behaviour suitability for nine of the ten butterfly species. All species demonstrated time- and age- independent survival rates. Species were found to differ significantly in longevity, encounter rate and behaviour suitability under exhibit conditions. Using the data and methodology of this study, exhibitors may select species to import based upon their relative cost-effectiveness and performance value.

Key words: Lepidoptera, live butterfly exhibits, life history, mark-recapture, longevity, survival rate.

Introduction

There are over 150 live butterfly exhibits worldwide, with the majority of exhibitors stocking their greenhouses with live pupae imported from tropical breeding farms (Brewster & Otis, 2009). Exhibitors must import pupae continuously throughout the year due to the relatively short lifespan of butterflies. These pupae represent hundreds of species varying in price from US$0.25-$5.00 per individual (personal communication with Wings of Paradise®). Imported butterflies also vary in longevity, visibility and behaviour, affecting their usefulness in exhibits (Watts, 2004). Some species engage in crowd-pleasing behaviours such as flying, feeding, or puddling, while others are cryptic or fly against windows, away from visitors. When importing pupae, exhibitors must balance the cost of the shipment with the appeal of the butterflies to their audience, importing both cost-effective and/or "crowd-pleasing" species.

Although there are a few existing studies documenting survival and encounter rates of butterflies in the wild (e.g. O'Brien *et al.*, 2003, survival of the pollen feeding *Heliconius charitonia*; Auckland *et al.*, 2004, survival and movement patterns of *Parnassius clodius*), there is a paucity of reliable estimates for butterfly longevity under exhibit conditions. Of the previous attempts to determine mean species lifespan in captivity (Kelson, 2002; Watts, 2004; Brewster & Otis, 2009), only Brewster and Otis implemented the appropriate mark-recapture analyses. Studies conducted by Kelson (2002) and Watts (2004) failed to control for variation in recapture success; therefore, individuals undetected during a sampling period may have been recorded as dead. Current mark-recapture methods estimate survival rate by controlling for the variation in recapture probability (the chance of recapturing an individual during a given sample

[1]*Current address:* Dept. of Biology, University of Toronto at Mississauga, Mississauga ON L5L 1C6, Canada.
laura.robson@utoronto.ca

Received: 14 October 2007
Accepted: 10 March 2008

period), thereby decreasing the likelihood that the mean survival rate would be underestimated (Altwegg *et al.*, 2003). Since the early 1990's, modeling programs such as SURVIVE, RELEASE and MARK have become popular tools for calculating population parameters using mark-recapture data (Nowicki *et al.*, 2005; O'Brien *et al.*, 2005). In this study, we estimated the survival rate of the captive butterflies using the maximum likelihood program MARK 4.2 (G.C. White, Colorado State University, Fort Collins CO).

To estimate the survival and encounter rates of a species, one must first determine whether these parameters change with time or age. Butterflies are heterothermic organisms and their activity is thought to depend on thermal conditions (Kemp, 2001). Because these environmental conditions could change daily, we predicted that butterfly encounter rate would be time-dependent. Observation at the conservatory suggests that the exhibited butterflies tend to be more active under clear skies and moderate temperatures (personal communication, Wings of Paradise®), supporting our prediction. Many individuals in the wild are thought to die from environmental risks such as diseases, predators and weather conditions; the stochastic nature of these factors may result in a survival rate that is roughly constant over time (Clements & Paterson, 1981, Speight *et al.*, 1999). In addition, a number of organisms, including some insects, have been shown to demonstrate age-dependent survival (Pollack, 1981; Harrington *et al.*, 2001; Aukland *et al.*, 2004). Nisbet and Cam (2002) argued that age dependence in survival rate reflects one of three phenomena: changes within individuals (experience and senescence with increasing age), age-specific emigration, or mortality selection (individuals in the older age classes have lower mortality risk due to selective survival). In a controlled conservatory setting with no immigration or emigration, only the first and third phenomena could provide valid explanations if age-dependent survival was observed among exhibited butterflies. Given the favourable conditions of a conservatory, where predation is usually absent and food is abundant, we predicted that exhibited butterflies would demonstrate age-dependent survival rates.

To estimate the comparable cost-effectiveness of imported species, Brewster and Otis (2009) developed a replicable mark-recapture protocol to estimate longevity, encounter rate and behaviour for Costa Rican and Malaysian butterflies. However, the life history parameters for many other butterfly species commonly imported by exhibitors have yet to be quantified. Data on these species will help exhibitors make informed decisions during butterfly selection. The objective of this research is to determine whether ten commonly imported Philippine butterfly species differ in their longevity, encounter rate and behaviour. By quantifying these variables, we can elucidate the relative cost-effectiveness of the species in exhibit conditions.

Methods

Ten species of Philippine butterflies (Table 1) were imported from M. A. Corona Butterfly Culture in Marinduque, Philippines, to Wings of Paradise® Butterfly Conservatory in Cambridge, Ontario. The butterflies studied were sent in two shipments,

Table 1. Scientific names, common names, family names and number of marked individuals of ten Philippine butterfly species imported for a mark-recapture study at Wings of Paradise® Butterfly Conservatory. Note that *Papilio deiphobus* is sold by the distributor as *Papilio rumanzovia* and *Atrophaneura kotzebuea* is sold as *Pachliopta kotzebuea*.

Species	Common name	Family	N
Atrophaneura kotzebuea (Eschscholtz, 1821)	Velvet Rose	Papilionidae	16
Cethosia biblis (Drury, 1773)	Red Lacewing	Nymphalidae	10
Danaus chrysippus (Linnaeus, 1758)	Plain Tiger	Nymphalidae	21
Graphium agamemnon (Linnaeus, 1758)	Tailed Jay	Papilionidae	23
Idea leuconoe Erichson, 1834	Ricepaper	Nymphalidae	117
Papilio deiphobus Linnaeus, 1758	Scarlet Mormon	Papilionidae	22
Papilio palinurus Fabricius, 1787	Emerald Swallowtail	Papilionidae	109
Papilio polytes Linnaeus, 1758	Common Mormon	Papilionidae	11
Parthenos sylvia (Cramer, [1775])	Clipper	Nymphalidae	120
Troides rhadamantus (Lucas, 1835)	Troides Birdwing	Papilionidae	16

arriving 13.VII.2006 and 20.VII.2006. We marked butterflies within three hours of emergence, once their wings had dried. Using a fine-point permanent marker, each butterfly was marked with a unique three-digit identification number on the underside of each of the four wings before being released into the conservatory.

We recaptured butterflies two to five times weekly, from 17.VII.2006 to 1.IX.2006. To account for the temporal variability in butterfly behaviour, we conducted three recapture sessions on each recapture day, from 9:00-10:00, 12:00-13:00 and 15:00-16:00. Results for the three recapture sessions were pooled for the day. We recaptured butterflies with a net as we walked a consistent circuit through the conservatory. The identification number, species and the behaviour prior to capture were recorded for marked individuals. If the same butterfly was captured more than once during a session, only the first recapture and behavior was recorded.

The program MARK 4.2 (G.C White, Colorado State University, Fort Collins CO) was used to estimate the survival probabilities (φ) and encounter probabilities (p) for each species using maximum likelihood estimation techniques. Survival rate is the probability that an individual will survive to the next day and encounter rate is the daily probability of recapturing an individual. The data-sets were modeled using the "recaptures only" Cormack-Jolly-Seber model (Cooch & White, 2006).

For each species, we tested seven models in MARK to determine the effects of time and age upon the survival and encounter parameters (Table 2). There are four assumptions inherent to the Cormack-Jolly-Seber model: a) all marked butterflies have the same probability of being recaptured at time (i); b) all marked butterflies have the same probability of surviving to time (i +1); c) identification markings are not lost and d) sampling is instantaneous relative to the amount of time between (i) and (i +1) (White & Burnham, 1999). Assumptions c) and d) were met because all markings were made with permanent ink and the butterflies were released immediately after each recapture. Assumptions a) and b) must be satisfied by accounting for lack of fit between the model and the data (Cooch & White, 2006). The candidate models were tested and compared using Akaike's information criterion (AIC) to identify the model giving the greatest balance of model fit and estimate precision (Akaike, 1981).

Lebreton *et al.* (1992) suggested that the AIC values can be adjusted for lack of fit using the variance inflation factor, $\hat{c}$, a measure of extra-binomial variation. The program RELEASE (a subroutine of the program MARK 4.2) was used to calculate the variance inflation factor for each species. A $\hat{c}$ value greater than three suggests that there is overdispersion in the data and indicates lack-of-fit for the model (Lebreton *et al.*, 1992). A $\hat{c}$ value less than one suggests that there is underdispersion in the data, likely due to the sparseness of the data set (Boyle & Flowerdew, 1993). The variance inflation value was used to modify the AIC value to give the quasi-likelihood adjusted AIC value, QAIC. The model giving the lowest QAIC value was considered the most parsimonious and was used to estimate the values of the survival and encounter parameters for the species.

Estimates for survival probability (φ) and standard error were used to determine mean adult lifespan and standard error for each species using the following formulae (Leisnham *et al.*, 2003): mean lifespan = -ln(φ)-1 and SE = ln (φ)-2 × SE(φ)÷ (φ). Both mean lifespan and mean encounter rate were compared between species using two-tailed t-tests.

Table 2. Candidate models for the estimation of the survival parameter (φ) and encounter parameter (p) for ten species of imported Philippine butterflies housed at Wings of Paradise® Butterfly Conservatory from July to September, 2006.

Model	Description
$\varphi.p.$	Survival rate and encounter rate are both constant over time.
$\varphi_t p.$	Survival rate is time dependent, encounter rate is constant over time.
$\varphi.p_t$	Survival rate is constant over time, encounter rate is time dependent.
$\varphi_t p_t$	Survival rate and encounter rate are both time dependent.
$\varphi_{age} p_{age}$	Survival rate and encounter rate are both age dependent.
$\varphi_{age} p.$	Survival rate is age dependent, encounter rate is age independent.
$\varphi.p_{age}$	Survival rate is age independent, encounter rate is age dependent.

Table 3. Estimates of longevity, encounter rate and behaviour suitability of ten species of Philippine butterflies housed at Wings of Paradise® Butterfly Conservatory from July to September, 2006. Standard error could not be calculated for species with time-dependent encounter rates.

Species	Longevity	± SE (Days)	Encounter rate	± SE	Behaviour suitability	± SE
Atrophaneura kotzebuea	4.2	1.2	0.47	0.11	0.52	0.16
Cethosia biblis	21.5	9.9	0.19	–	1.00	0.00
Danaus chrysippus	10.0	2.6	0.37	–	0.68	0.12
Graphium agamemnon	NA	NA	NA	NA	1.00	0.00
Idea leuconoe	28.3	4.0	0.48	–	0.88	0.03
Papilio deiphobus	18.8	6.5	0.26	0.04	0.88	0.08
Papilio palinurus	7.8	1.1	0.20	–	0.92	0.04
Papilio polytes	8.9	3.7	0.47	0.09	0.75	0.19
Parthenos sylvia	16.0	1.9	0.29	–	0.95	0.02
Troides rhadamantus	13.9	5.5	0.40	0.06	0.96	0.04

Table 4. Comparisons between nine imported Philippine butterfly species for mean longevity and behaviour suitability. Presence of a symbol indicates a significant difference in longevity (γ) or behaviour suitability (*) between each pair of species (two-tailed t-test, $p < 0.05$). Data were collected using a mark-recapture protocol at Wings of Paradise® Butterfly Conservatory from July to September, 2006. None of the species with time-independent encounter probabilities exhibited significantly different encounter rates. Encounter rates were not compared among species with time-dependent encounter probabilities.

	A. kotzebuea	*C. biblis*	*D. chrysippus*	*I. leuconoe*	*Pap. deiphobus*	*Pap. palinurus*	*Pap. polytes*	*Par. sylvia*
A. kotzebuea	-							
C. biblis	*	-						
D. chrysippus	γ	*	-					
I. leuconoe	γ	*	γ	-				
Pap. deiphobus	γ				-			
Pap. palinurus	γ*	*		γ		-		
Pap. polytes				γ			-	
Par. sylvia	γ*	*	*	γ*		γ		-
T. rhadamantus	*		*	γ				

We categorized observed butterfly behaviour as either suitable or unsuitable upon each recapture depending on whether or not it enhanced the aesthetic appeal of the exhibit. Suitable behaviours included: sitting on foliage, feeding on fruit or flowers, flying, copulating, ovipositing, puddling or sitting on a visitor. Unsuitable behaviours included: flying or sitting near the windows or roof and conspicuous moribundity. For each species, we calculated the proportion of time spent performing suitable behaviours. Average behaviour suitability was calculated for each individual of a species and the mean of these individual averages was used as the behaviour suitability score for that species. Mean behaviour suitability rate was compared between species using two-tailed t-tests.

Results

Model selection: of the ten species studied, *D. chrysippus*, *P. palinurus*, *I. leuconoe*, *P. sylvia* and *T. rhadamantus* all had a variation inflation factor within the $1< \hat{c} <3$ range indicating model goodness-of-fit. *C. biblis*, *A. kotzebuea*, *P. deiphobus* and *P. polytes* all had $\hat{c}$ values less than one, indicating underdispersion of the data. For underdispersed data, Cooch and White (2006) suggest setting these inflation variance values to $\hat{c}=1$ for the purposes of calculating QAIC. The program RELEASE was unable to calculate the $\hat{c}$

value for *Graphium agamemnon* due to the infrequency of encounters following their release. This resulted in data too sparse to model using program MARK. Therefore, we were unable to estimate survival or encounter parameters for *G. agamemnon* and it was subsequently omitted from our analyses.

A summary of the results on butterfly longevity, encounter rates and behaviour suitability is presented in Table 3.

Survival probability: the survival probabilities of all nine species were independent of both time and age.

Longevity: of the 36 comparisons of mean longevities among species, 11 differed significantly. (Table 4). *I. leuconoe* had a longevity of 28.5 ± 9.9 days, which was significantly longer than that of six of the eight other species. *A. kotzebuea* had the shortest longevity of 4.2 ± 1.3 days. This was significantly shorter than the longevities of five of the other eight species (Table 4).

Encounter probability: of the nine butterfly species modeled, five had encounter probabilities that varied with time (Table 3). For these five species, the probability of encounter changed daily and there was no single mean value with an associated standard error to compare among species. All five of these species had the lowest encounter probabilities on 17.VII.2006, 18.VII.2006, 2.VIII.2006 and 3.VIII.2006. The remaining four species had time- and age-independent encounter probabilities. The probability of encounter was not found to differ significantly among these four species with time-independent encounter rates.

Behaviour Suitability Rate: all butterfly species exhibited more suitable behaviours than non-suitable behaviours. There were significant differences in behaviour suitability rate between 11 of the 36 pairs of species (Table 4). *C. biblis* had the highest behaviour suitability rate of 1.00 ± 0.00 suitable behaviours/total observed behaviours, which was significantly higher than that of five other species. *A. kotzebuea* had the lowest behaviour suitability rate of 0.52 ± 0.15 suitable behaviours/total observed behaviours, significantly lower than that of four other species (Table 4). The low behaviour suitability value of *A. kotzebuea* was due to the large proportion of observation periods in which individuals of this species were seen sitting at the windows away from the public.

Discussion

Of the nine species of Philippine butterflies for which survival and encounter rates were estimated, all demonstrated significant differences in their life history parameters and therefore, their suitability for use in live exhibits. *Idea leuconoe* had an extremely long lifespan, while *Papilio polytes* was relatively short-lived, but exhibited high behavior suitability (Table 3). The encounter data for *Graphium agamemnon* were too sparse to estimate survival and encounter parameters using program MARK. Of the 23 marked *G. agamemnon* individuals, 14 were never seen again after their initial release and the remaining nine were rarely encountered more than once. While we were unable to generate parameter estimates for this species, the extremely low encounter rate suggests that *G. agamemnon* is an inappropriate species for live exhibition.

No single species was significantly superior to all others in all three measures (longevity, encounter rate and behaviour suitability rate). Therefore, the value of the species to an exhibit depends on the relative weight given to the parameters deemed most important by the exhibitor.

The time- and age-constant survival probabilities observed for all ten Philippine species indicate that the butterflies died at a constant rate. Time- and age-independent survival is believed to be typical for many insects in the field where mortality is predominantly caused by predation and disease rather than senescence or environmental conditions (Clements & Paterson, 1981; Tsuda *et al.*, 2001). The time- and age-constant rate of survival that we observed was surprising given the generally risk-free conditions in the conservatory. Among the factors that may have influenced survival are improper larval nutrition, disease, and predation. Larval nutrition has been found to contribute to the survival of adult butterflies (Boggs & Freeman, 2005); therefore, it is possible that variable larval growth conditions at the tropical rearing farms contributed to the age-independent probability of adult survival. Diseases contracted during the larval stage may have manifested during the adult stage and this too may have contributed to the constant survival rate. Predation at Wings of Paradise®, which we initially assumed was non-existent, may have been greater than expected, resulting in mortality rates that were constant for all ages of butterflies. Possible predators were ants, frogs, spiders of several species that colonize the conservatory, or the finches and Chinese painted quail on exhibit.

Two separate shipments were pooled for the calculation of longevity, encounter rate and behaviour suitability. Ideally, the mark-recapture protocol used in this study could be repeated for each of several shipments in order to determine the consistency of the estimated parameters. Potential variability between shipments could be attributed to differences

Table 5: Total number of suitable days, cost per pupa and cost per day for nine species of Philippine butterflies housed at Wings of Paradise® Butterfly Conservatory from mid July to 1 September, 2006. Total number of suitable days was calculated as the product of species longevity × average encounter rate × behaviour suitability rate. Cost per day for a species was calculated as cost per pupa ÷ total number of suitable days.

Species	Total suitable days	Cost (USD)	Cost/Day (USD)
Atrophaneura kotzebuea	1.0	$ 0.60	0.60
Cethosia biblis	4.1	$ 0.40	0.10
Danaus chrysippus	2.5	$ 0.40	0.16
Idea leuconoe	11.9	$ 0.60	0.05
Papilio deiphobus	4.3	$ 0.80	0.19
Papilio palinurus	1.4	$ 0.80	0.57
Papilio polytes	3.1	$ 0.40	0.13
Parthenus sylvia	4.4	$ 0.60	0.13
Troides rhadamantus	5.3	$ 0.80	0.15

in larval rearing conditions (Boggs & Freeman, 2005) or variation in shipping conditions. These pre-arrival influences can also affect the percentage of pupal losses suffered by each species. Butterflies may either arrive dead or emerge improperly due to premature eclosion during shipment, improper shipping temperature, parasitism, disease and mishandling (personal communication with Wings of Paradise®). Although it was not quantified in this study, mean species pupal loss could be used in conjunction with survival, encounter rate and behaviour suitability to provide a more comprehensive estimate of cost-effectiveness for each species.

All five species with time-dependent encounter rates had extremely low encounter probabilities on the same four sampling days (17.VII.2006, 18.VII.2006, 2.VIII.2006 and 3.VIII.2006). The first three dates were extremely hot, humid and sunny, while the last date was dark and rainy. Because butterflies are heterothermic organisms, their flight and activity are constrained by the thermal conditions (Kemp, 2001). While a minimum temperature is required for the butterflies to meet the metabolic demands of flight, Douglas (1986) suggested that in extremely hot conditions, butterflies thermoregulate by resting in shaded areas, which leads to a decrease in their encounter probability. While the environmental conditions of Wings of Paradise® are much less variable than ambient conditions, our results suggest that the temperatures and light levels in the conservatory sometimes fall outside the range suitable for activity of these Philippine species. Tighter regulation of the microclimate within the exhibit may aid in increasing the encounter probability and subsequently the cost-effectiveness of exhibited butterflies.

The butterfly species we studied did differ in life history traits. Exhibitors may use these life history values to select species which best display the desired characteristics. For example, an exhibitor may choose to import a substantial number of long-lived, highly visible species such as *I. leuconoe*. These could be supplemented with a variety of species exhibiting visitor-pleasing behaviours, such as the flower-visiting behaviour of *C. biblis*. By eliminating the importation of species with low life-history parameter values, exhibitors may either decrease importation costs or redirect funds toward increasing apparent butterfly abundance through the importation of species with higher life history parameter values. Exhibitors must also consider the overall appeal of the exhibit, a qualitative value not estimated in this study. Some visitors may appreciate high species diversity whereas others may prefer large or colourful species or large numbers of individuals.

Brewster and Otis (2009) calculated a cost-effectiveness score for exhibited Costa Rican and Malaysian butterfly species using the following formula: species cost-per-day = total suitable days ÷ price, where total suitable days = longevity × encounter rate × behaviour suitability. Using this formula, cost-effectiveness values were calculated for the nine Philippine butterfly species in this study with interesting results (Table 5). *Idea leuconoe* demonstrated the greatest number of suitable days per unit of cost, while *Atrophaneura kotzebuea* was the least cost-effective species. *Troides rhadamantus* and *Papilio deiphobus*, while among the most expensive species to purchase ($0.80/pupa), had cost-per-day values three to five times lower than *Atrophaneura kotzebuea* pupae ($0.60 per pupa). Note that this index does not have an associated standard error to account for within-species variation. However, it does allow exhibitors to integrate several life-history parameters into a single value that facilitates the comparison of cost-effectiveness among species.

Conditions that improve any of these three life-history parameters for one or more species will improve the cost-effectiveness of the exhibit. The improvement and addition of fresh and/or fermented fruit, floral and sugar-rich resources may serve to increase the longevity and encounter rates of many species. For example, it is widely accepted that pollen feeding greatly enhances adult longevity and fecundity for neotropical *Heliconius species* (Boggs *et al.*, 1981; O'Brien *et al.*, 2003). Placement of feeding stations towards the interior of the conservatory may help to move individuals away from the windows. Additionally, conservatories may use either exclusion netting or specialized ventilation systems that circulate air to the centre of the greenhouse to keep butterflies away from windows. Implementation of these methods may serve to increase encounter rates and butterfly behaviour suitability. The effects of these interventions could be determined with the mark-recapture protocol employed in this study.

In summary, Philippine butterfly species differ in their longevity, encounter rate and behaviour suitability and therefore differ in their cost-effectiveness in live exhibits. The elucidation of these life history parameters enables exhibitors to make informed decisions regarding the species they import.

Acknowledgements

Financial support for this project was provided by a Natural Science and Engineering Research Council undergraduate student research award (USRA). Thanks to Wings of Paradise® Butterfly Conservatory for providing the butterflies and allowing for the use of their facility.

Literature Cited

Akaike, H. 1981. Likelihood of a model and information criteria. Journal of Econometrics 16: 3-14.

Altwegg, R., A. Roulin, M. Kestenholz & L. Jenni. 2003. Variation and covariation in survival, dispersal and population size in barn owls *Tyto alba*. Journal of Animal Ecology 72: 391-399.

Aukland, J. N., D. M. Debinski & W. R. Clark. 2004. Survival, movement, and resource use of the butterfly *Parnassius clodius*. Ecological Entomology 29: 139-149.

Boggs, C. L. & K. D. Freeman. 2005. Larval food limitation in butterflies: effects on adult resource allocation and fitness. Oecologia 144: 353-361.

Boggs, C. L., J. T. Smiley, & L. E. Gilbert. 1981. Patterns of pollen exploitation by *Heliconius* butterflies. Oecologia 48: 284-289.

Boyle, P. & R. Flowerdew. 1993. Modeling sparse interaction matrices: interward migration in Hereford and Worcester, and the underdispersion problem. Environment and Planning A 25: 1481-1510.

Brewster, A. L. E. & G. W. Otis. 2009 (In press). A protocol for evaluating cost-effectiveness of butterflies in live exhibits. Journal of Economic Entomology 102.

Clements, A. N. & G. D. Paterson. 1981. The analysis of mortality and survival rates in wild populations of mosquitoes. Journal of Applied Ecology 18: 373-399.

Cooch, E. & G. White. 2006. Program MARK: a gentle introduction (4th edition). Accessed 14 July, 2006, http://www.phidot.org/software/mark/docs/book.

Douglas, M. M. 1986. The lives of butterflies. University of Michigan Press, Ann Arbor, MI.

Harrington, L. C., J. P. Buonaccorsi, J. D. Edman, A. Costero, P. Kittayapong, G. G. Clark & T. W. Scott. 2001. Analysis of survival of young and old *Aedes aegypti* (Diptera: Culicidae) from Puerto Rico and Thailand. Journal of Medical Entomology 38: 537-547.

Kelson, R. 2002. Longevity of tropical butterflies in a butterfly house in California. Proceedings of the Invertebrates in Captivity Conference, 2002: 169-177.

Kemp, D. J. 2001. Investigating the consistency of mate-locating behaviour in the territorial butterfly *Hypolimnas bolina* (Lepidoptera: Nymphalidae). Journal of Insect Behaviour 14: 129-147.

Lebreton, J. D., K. P. Burnham, J. Clobert & D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: case studies and recent advances. Ecological Monographs 62: 67-118.

Leisnham, P. T., C. Cameron & I. G. Jamieson. 2003. Life-cycle, survival rates and longevity of an alpine weta *Hemideina maori* (Orthoptera: Anostostomidae) determined using mark-recapture analysis. New Zealand Journal of Ecology 27: 191-200.

Nisbet, I. C. T. & E. Cam. 2002. Test for age-specificity in survival of the common tern. Journal of Applied Statistics 29: 65-83.

Nowicki, P., A. Richter, U. Glinka, A. Holzschuh, U. Toelke, K. Henle, M. Woyciechowski & J. Settele. 2005. Less input same output: simplified approach for population size assessment in Lepidoptera. Population Ecology 47: 203-212.

O'Brien, D. M., C. L. Boggs & M. L. Fogel. 2003. Pollen feeding in the butterfly *Heliconius charitonia*: isotopic evidence for essential amino acid transfer from pollen to eggs. Proceedings of the Royal Society of London B. 270: 2631-2636.

O'Brien, S., R. Bourou & H. Tiandry. 2005. Consequences of violating the recapture duration assumption of mark-recapture models: a test using simulated and empirical data from an endangered tortoise population. Journal of Applied Ecology 42: 1096-1104.

Pollack, K. H. 1981. Capture-recapture models allowing for age-dependent survival and capture rates. Biometrics 37: 521-529.

Speight, M. R., M. D. Hunter & A. D. Watt. 1999. Ecology of insects: concepts and applications. Blackwell Science, Oxford. 125-130.

Tsuda, T., M. Takagi, S. Wang, Z. Wang & I. Tang. 2001. Movement of *Aedes aegypti* (Diptera: Culicidae) released in a small isolated village on Hainan Island, China. Journal of Medical Entomology 38: 93-98.

Watts, J. R. 2004. Longevity studies in a tropical conservatory: are you getting your money's worth? Proceedings of the Invertebrates in Captivity Conference, 2004: 39-45.

White, G. C. & K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46 (Supplement): 120-138.